

49. On the Feet and other External Features of the Canidæ and Ursidæ. By R. I. POCKOCK, F.R.S., F.L.S., F.Z.S., Curator of Mammals.

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(Text-figures 1-13.)

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Family CANIDÆ.

Apart from the feet, the external features dealt with in this paper are the rhinaria and the facial vibrissæ.

The feet of the typical Canidæ are highly specialised, and show a close adaptive resemblance to those of the Felidæ in the form of the plantar pad, the strong curvature of the line of the pads of digits two to five, in the backward position of the first digit of the fore foot, its absence from the hind foot, the hairiness of the area behind the plantar * pads, and the persistence of the single carpal pad on the fore feet. In their structural uniformity within the families, the feet of the Canidæ and Felidæ show a marked contrast to those of the Viverridæ, Mustelidæ, Procyonidæ, and Ursidæ.

In most wild species of Canidæ the feet differ only in minor points from those of domestic breeds already described †. The four principal digits are united by integument up to the base of the pads. The webbing thus formed may be wide or narrow, and clothed with longer or shorter hairs, according to the species. As in other Fissiped Carnivora, the hair grows in tufts between the pads of the feet and on the upper side of the webs. It is usually thickest and longest on the webs, the underside of the digits themselves showing a naked or nearly naked streak.

The *rhinarium* is always large and moist, there being apparently very little variation with respect to the extent to which the hair of the muzzle encroaches upon it. The upper lip below it is always divided by a narrow moist distensible area, which presents the form of a mere slit when its hairy margins are approximated in the middle line.

The normal tufts of *facial vibrissæ* are always present, but the

* I use this term indifferently for the main pad of both fore and hind feet.

† P. Z. S. 1914, pp. 478-484. The method adopted in that case of ascertaining the extent of the web by cutting the hairs short has been followed in the present communication dealing with the feet of the wild species of Canidæ and with the Ursidæ. The figures represent the paws with the hairs cut and the digits distended.

vibrissæ vary in length and number according to the species. The interramal tuft is placed nearly in a vertical line with the corner of the mouth when closed. As in most Fissiped Carnivores, there are two genal tufts, one behind the corner of the mouth, nearly in a vertical line beneath the posterior canthus of the eye, the other usually much higher up the cheek and farther back.

The genera of Canidæ hitherto established and admitted rest mainly upon cranial and dental characters.

Speothos venaticus Lund.

(Text-fig. 1, A, B.)

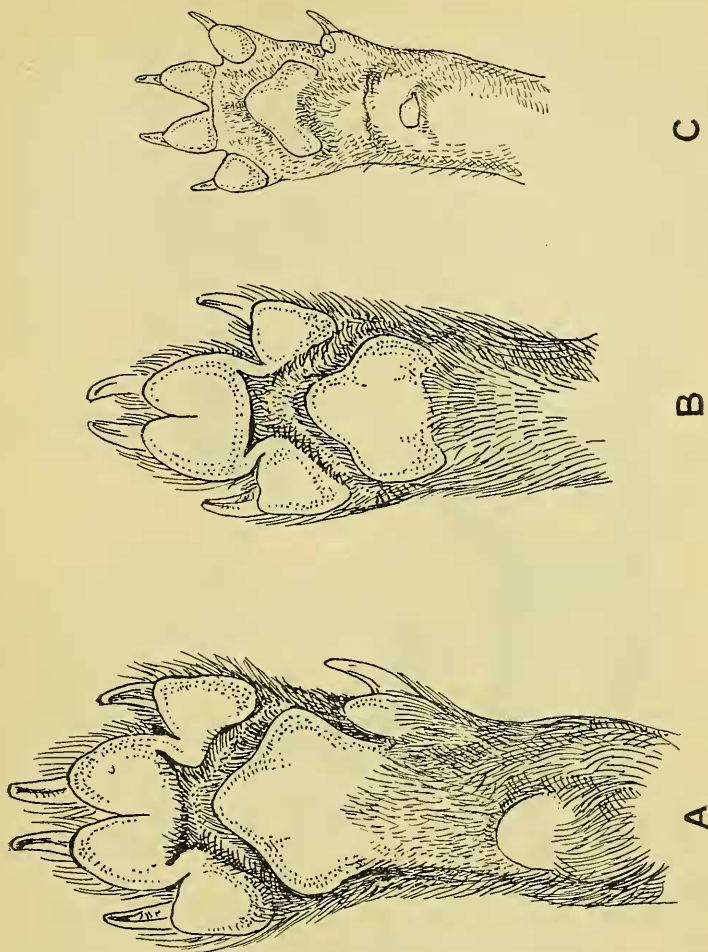
The feet of this rare dog, of which I have only been able to see dried skins, were figured by Flower (P. Z. S. 1880, p. 70), who dismissed them with a mere reference, and this figure was reproduced by Mivart in his 'Monograph of the Canidæ' (p. xv.) to illustrate the structure of the feet characteristic of that family. As a matter of fact, the feet differ from those of all other genera of the Canidæ in two very important particulars, namely, the extensive basal fusion of the third and fourth digital pads of both the front and hind feet, and the approximation of the digital pad of the first digit of the fore foot to the inner proximal angle of the plantar pad. Moreover, the area between the large plantar and the carpal pads of the fore foot is somewhat scantily hairy, especially externally, where a nearly naked strip of integument passes from pad to pad, and the edges of the interdigital integument connecting the second and third and the fourth and fifth digits is naked on both the anterior and the posterior paws, and the area between the digital and plantar pads appears to be sparsely covered with short hairs*.

From its low position, the first digit, it seems, must reach the ground when the animal is standing in the normal position, especially if the soil be soft. Coupled with the scantiness of the hairy clothing of the area above or behind the plantar pad, this suggests that *Speothos* is more plantigrade than any other existing dog; and it may be recorded in this connection that the mother of a specimen sent to the Gardens in 1879 (P. Z. S. 1879, p. 664) was killed in a creek and that two of the skins in the British Museum are labelled "Shot while running along creek."

If this dog habitually haunts the borders of streams, its plantigrade and scantily hairy feet must be an advantage for progression on sandy or muddy banks. It appears to me to be impossible

* Except for the forward position of the first digit and the fusion of the third and fourth digital pads in the fore foot, Flower's figure does not show these features well, and it is noticeable that the third and fourth digital pads on the hind foot are represented as separated throughout. The shape of the pads too and the median position of the carpal pad throw doubt upon the reliability of the figure. Hence it may be that the very marked asymmetry between the second and fifth digits on both feet is also exaggerated. But since the figure was taken from a fresh example that point may be correct. If so, it is full of interest; but on dried skins I cannot find convincing evidence that the second digit is so far in advance of the fifth as Flower's figure indicates.

Text-figure 1.



A. Right fore foot of *Speothos venaticus*, from dried skin.
 B. Right hind foot of same.
 C. Right fore foot of newly-born cub of *Canis pallipes*, showing the low position of the pollex.

to decide whether the peculiarity of the feet in the matter of the low position of the first digit and carpal pad is a secondarily acquired adaptation to conditions or whether it is a retained primitive character. I incline to the latter opinion, because these peculiarities are present in the newly born pups of species of dogs with normal feet when adult (text-fig. 1, C)*.

* In Lund's original figure of *Sp. venaticus* (Kongl. Danske Vid. Selsk. xi. pl. 61, 1845) the first digit is shown in its correct position, but there is a broad web between the remaining four, giving a palmate appearance to the spread paw, which is certainly inaccurate so far as the third and fourth digits are concerned.

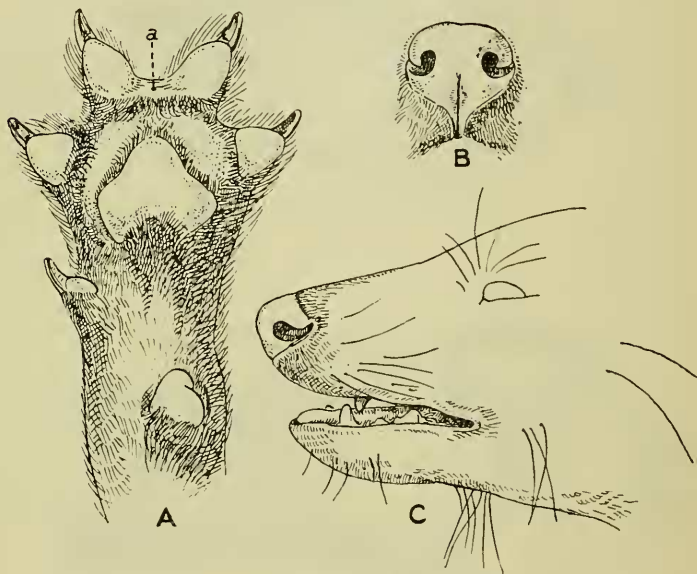
Cuon primævus Hodgs.

(Text-fig. 2.)

Apart from Blanford's brief reference to the feet of this species, which he described as having "long hair between the foot-pads," I am not acquainted with any description of them.

I have only seen the feet of two puppies, about four months old. In the relative positions of the carpal and plantar pads and the pad of the first digit, the fore foot resembles that of *Canis anthus* tolerably closely, but the carpal pad is longer and more prominent. Marked differences are noticeable in connection

Text-figure 2.

*Cuon primævus*.

- A. Left fore foot.
- B. Rhinarium from the front.
- C. Side view of face, showing vibrissæ and rhinarium.

with the four main digits. The third and fourth are widely separable, the space between them when distended being equal to that between the second and third and the fourth and fifth. The edge of the web joining them is smooth and not sharply differentiated from them by the hairy covering seen in most species of *Canidæ*. The edge of the web between the second and third and fourth and fifth digits, is not naked and forms a tolerably evenly curved line. The greater part of the sole between the four digital pads and the broadly cordate plantar pad is

scantly hairy, but laterally, close to the proximal margins of the pads and behind the naked rim above described, the hair grows in the form of a long fringe. This combination of features is only found in one other dog that I have examined, namely, *Lycaon pictus*.

Similar features are presented by the hind foot, which, however, is thinner and longer than the fore foot, the third and fourth toes being more prominent and less widely separable and the plantar pad narrower.

The *rhinarium* is bluntly rounded in profile view. Its inferior edge seen from the front is strongly angular, the margin below the nostrils being deep anteriorly and narrow and shallow posteriorly beneath the slit; the nostrils are smallish and widely spaced, and the median groove does not extend up between them.

The *facial vibrissæ* are normal in position and of moderate length, and in the specimen examined the superior genal tuft consisted of two unusually widely spaced bristles.

Lycaon pictus Temm.

(Text-fig. 3.)

A single example of *L. pictus sharicus* examined.

The main peculiarity about the feet of this dog, namely, the suppression of the first digit of the fore foot, is well known, but I am not aware that other characters have been recorded.

In one feature at least the fore foot recalls that of *Vulpes vulpes*, namely, in the length and narrowness of the area between the plantar and carpal pads, but here the resemblance ceases, for both these pads are large, as in *Canis*.

The paw itself is strikingly like that of *Cuon*, except that the digits are longer. Very suggestive of kinship between the two genera are the equality in the spacing of the four toes, due to the comparatively wide separation between the third and fourth digits, the nakedness of the edge of the web which joins these two digits together, and the great length of the hairs fringing the proximal margin of the digital pads, and the scantiness of the hairs clothing the sole between the plantar pad and these fringes.

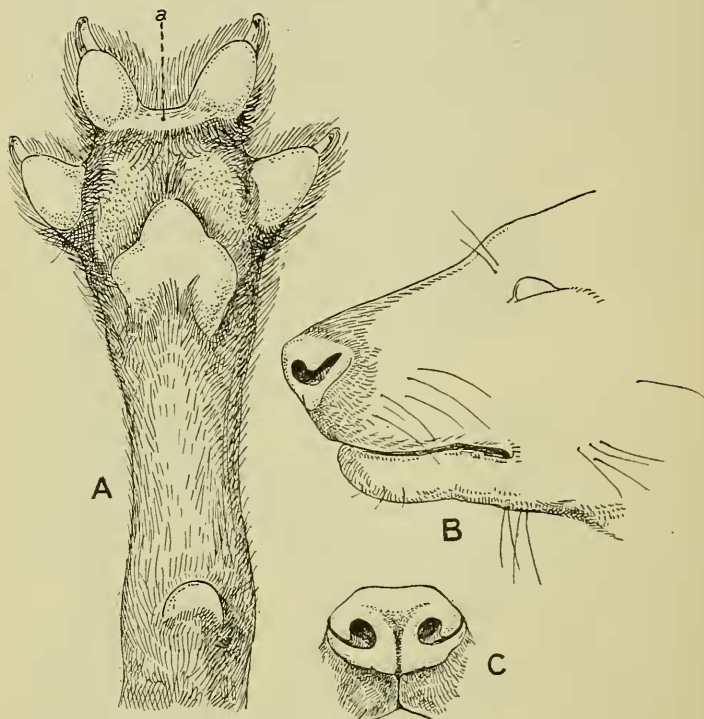
The hind foot is like the front, but is narrower and not so widely splayed.

The chief interest attaching to the feet of *Lycaon* is their likeness in the particulars mentioned to those of *Cuon*, especially as kinship between these two has been suggested on other grounds.

The *rhinarium* is large and wide, rounded anteriorly in profile view; its upper and lower edges parallel and transverse when seen from the front, the inferior edge sinuous and without any marked median inferior prolongation. The nostrils are large, rounded, and somewhat widely separated, the posterior slit of the nostril is bordered below at its posterior end by a thick area of

moist black integument; a somewhat deep median groove extends between the nostrils upwards from the cleft of the upper lip. This rhinarium is very different from that of *Cuon* and the other species and genera of *Canidæ* examined.

Text-figure 3.

*Lycaon pictus.*

- A. Left fore foot. *a*. Naked margin of web joining third and fourth toes.
 B. Lateral view of face, showing rhinarium and vibrissae.
 C. Rhinarium from the front.

Facial vibrissæ short and not numerous, except that the interramal and inferior genal tufts, which are normal in position, consist of about four bristles each. The superior genal, consisting of one bristle only, is set much lower than in other *Canidæ*.

Canis anthus Linn.

(Text-fig. 4, A, B.)

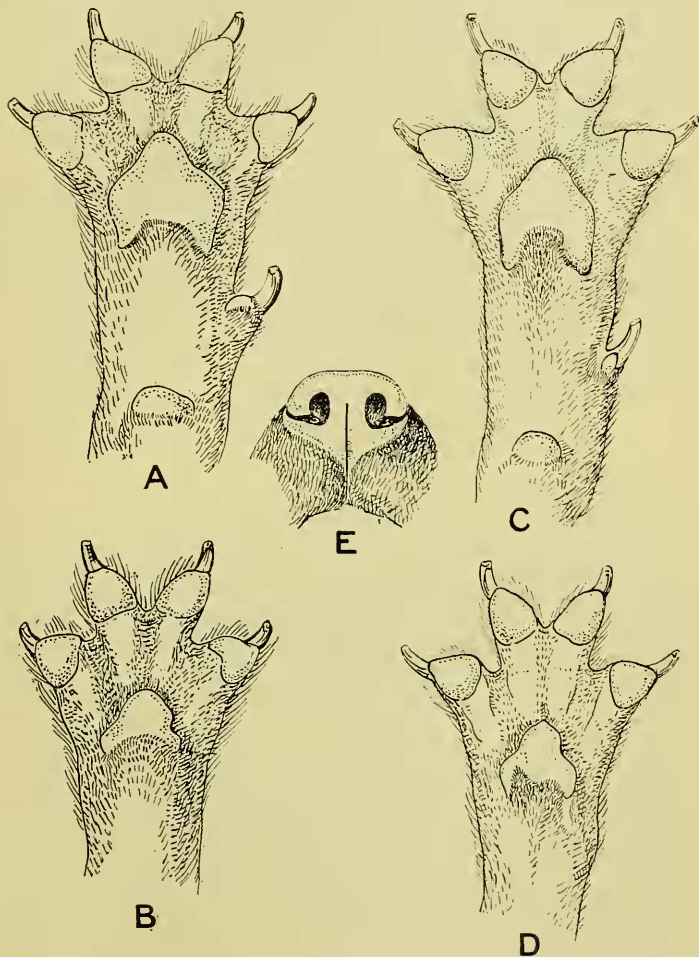
A single example of this Jackal from Morocco.

Fore feet short, especially the third and fourth digits, which

are somewhat tightly tied together, the distance between them much less than that which separates them from the second and fifth respectively. Digital pads moderately large; plantar pad large, both long and wide. Carpal pad large, wider than long.

Hind foot with digits less widely spread than those of front foot, plantar pad much smaller both in width and length.

Text-figure 4.



Canis anthus and *C. mesomelas*.

- A. Right fore foot of *Canis anthus*. C. Right fore foot of *Canis mesomelas*.
 B. Right hind foot of same. D. Right hind foot of same.
 E. Anterior view of rhinarium of *C. mesomelas*.

Canis mesomelas Schreb.

(Text-fig. 4, C-E.)

The fore foot of this species is considerably more "foxy" in form than that of *Canis anthus*. The area between the carpal and plantar pads is longer and narrower, the carpal pad is smaller, the plantar pad is narrower and more overgrown with hairs in the middle behind; the area between the plantar pad and the notch between the third and fourth digits is longer, the pads of these digits are tied more tightly together, and the edge of the web between them and the lateral digits is more deeply emarginate.

The hind foot differs from the fore foot in the smallness of the plantar pad and in the still deeper emargination of the edge of the lateral web.

The *rhinarium* is acutely rounded anteriorly in profile; from the front view its upper edge is straight with obtusely rounded angles, and its lower edge acutely angled mesially with obliquely sloping sides, the area beneath the nostrils in front being somewhat shallow and becoming progressively shallower laterally and posteriorly beneath the narial slit.

The *facial vibrissæ* are normal in position and moderately long (see *supra*, p. 901).

Cerdocyon microtis Slater.

(Text-fig. 5.)

= *Canis slateri* Allen.

A single specimen from the Amazons.

Fore feet longer and more loosely webbed than in *C. anthus*, the third and fourth digits joined by a wider web, the distance between them only a little less than that between the second and third and fourth and fifth. Plantar pad large, but rather smaller relatively than in *C. anthus*, its median lobe wider and rounder. Carpal pad high up, very small, and conical. Claws short.

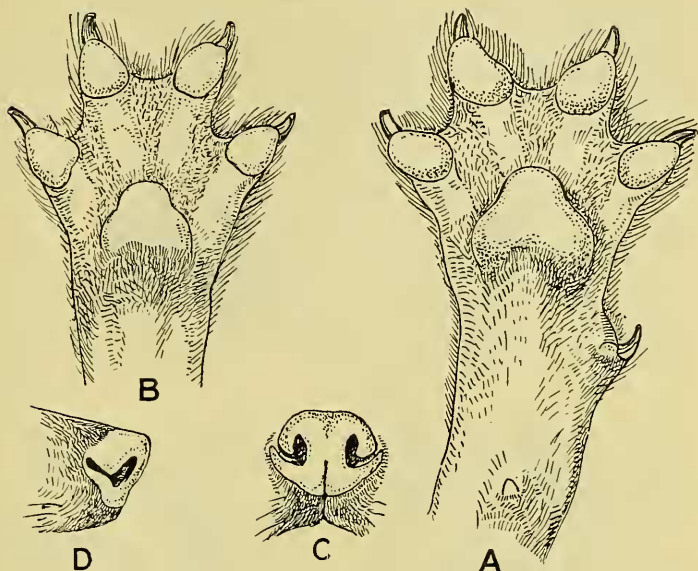
Hind feet longer and narrower than fore feet and with smaller plantar pad, the posterior borders of the pad not deeply emarginate. Hairs between the pads thick, but not specially long.

The *rhinarium* is nearly rectangular anteriorly in profile view. Seen from the front its upper edge is straight and transverse with rather widely rounded angles; its inferior edge is strongly and tolerably evenly convex, owing to the great depth of the portion below the nostrils in front, the portion below the slit of the nostrils behind narrow; hairy area of the lip below the rhinarium shallow, its median slit continued upwards on to the rhinarium as a groove which ascends a little higher than the inferior rim of the nostrils.

The *facial vibrissæ* moderately long—shorter, that is to say, than in *C. mesomelas*, *Ps. gracilis*, and the species of *Vulpes*; normal in position, except that the superior genal tuft, consisting of two

bristles, is set unusually high, nearly on a level with the posterior canthus of the eye.

Text-figure 5.



Cerdocyon microtis.

A. Right fore foot.
B. Right hind foot.

C. Rhinarium from the front.
D. Rhinarium from the side.

Points to be noticed in connection with this species, apart from the remarkably small size of the ears, which are only $2\frac{1}{4}$ inches (56 mm.) long*, are the comparatively wide and nearly even spacing of the digital pads when stretched, the very small size of the carpal and pollical pads, the depth of the rhinarium below the nostrils in front, and the high position of the superior genal vibrissæ.

* Most of the South American dogs have the ears as long relatively as in typical foxes (*Vulpes vulpes*), which about equal *Cerdocyon microtis* in size and have a skull of about the same length. But, according to Miller, the ears of *V. vulpes* range from 82 to 98 mm.

The cæcum in this example of *C. microtis* was short and uncoiled as recorded by Garrod of *C. cancrivorus* (= *C. thous*), and there is very little doubt that these two species are tolerably closely related. On the other hand, in the specimen of *Ps. gracilis* from Cordova and in an example of *Ps. azaricus* from Mar del Plata, the cæcum was longer and coiled, as described by Garrod of *C. antarcticus*. There are discrepancies in the accounts of the cæcum of *C. azaræ*, Mivart stating it to be straight and Garrod stating it to be coiled. The name *azaræ*, however, has been given to at least two distinct species, one belonging to the *thous*- or *cancrivorus*-group and another to the *culpæus*-group of South American dogs (see Thomas, Ann. Mag. Nat. Hist. (8) vol. xiii. p. 345, 1914). No doubt, Mivart and Garrod had different species under examination, and that Mivart's determination was probably correct may be surmised from the fact that true *azaræ* belongs to the *thous*-group.

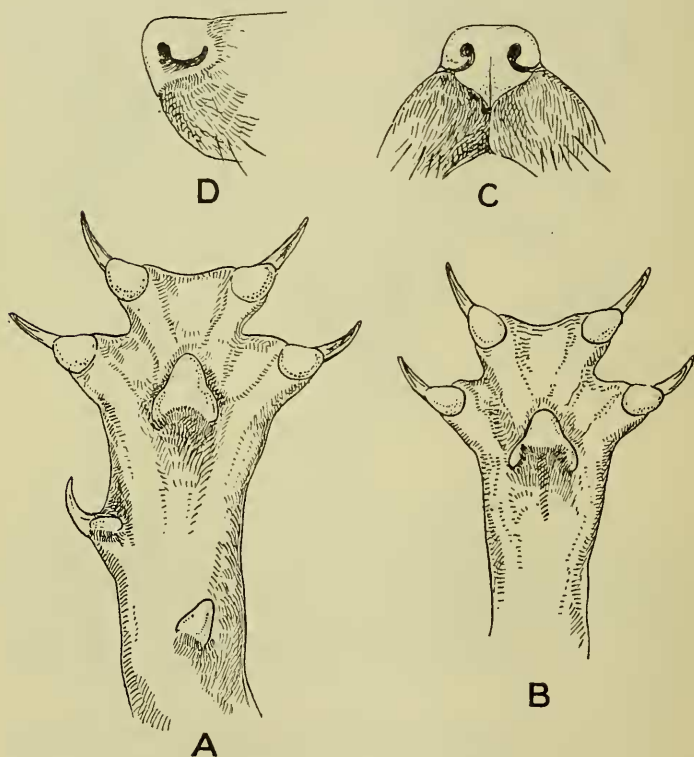
Pseudalopex gracilis Burm.?*

(Text-fig. 6.)

A half-grown specimen of this or an allied species of the *culpæus*-group from Cordova.

Feet long, the small conical carpal pad high above the plantar pad, the pad of the first digit about on a level with the mid-point

Text-figure 6.

*Pseudalopex gracilis*?

A. Left fore foot.
B. Left hind foot.

C. Rhinarium from the front.
D. Rhinarium from the side.

between the two. Plantar pad long as compared with its width, narrowly cordate with deeply emarginate posterior border. The digits moderately long, with small pads and unusually distensible,

* Typical *gracilis* came from Mendoza. Hence the determination of this young individual is a little uncertain.

so that the foot is extraordinarily wide when spread to the fullest extent, the third and fourth capable of being separated until the inner edges of the pads are in a transverse, almost straight, line with the border of the web connecting them which is only lightly emarginate, the width of this web about twice the length of one of the pads and exceeding the distance between the pads of the second and third or fourth and fifth digits. Claws long and slender. The hairs on the lower surface of the foot abundant, silky, and long, completely concealing the pads when undisturbed.

Hind foot very like the fore foot, but smaller, the posterior portion of the plantar pad more overgrown with hairs.

The *rhinarium* is rectangularly rounded in front in profile; from the front view its upper edge is wide and straight with nearly rectangularly rounded angles, its inferior border is mesially angular with obliquely sloping, slightly sinuous sides, the area below the nostrils being moderately deep in front and narrow posteriorly below the slit; the hairy area of the lower lip below the rhinarium in front is moderately deep and the cleft is continued upwards as a shallow groove between the nostrils.

The *facial vibrissæ* are long and abundant and normal in position, about six superciliaries, three interramals, and three to each of the genal tufts. In an example of *Ps. azaricus* from Mar del Plata, the vibrissæ resemble those of the species above identified as *Ps. gracilis*.

The feet of *Ps. gracilis* suggest adaptation to desert conditions, the spread of the digits and the thick hairy clothing preventing sinking in the sand.

It will be interesting to see in the future to what extent the feet of the other fox-like South American dogs, such as *Ps. culpæus*, conform to this type, which differs so widely from that of some of the true foxes of the Old World, like *Vulpes* and *Otocyon*.

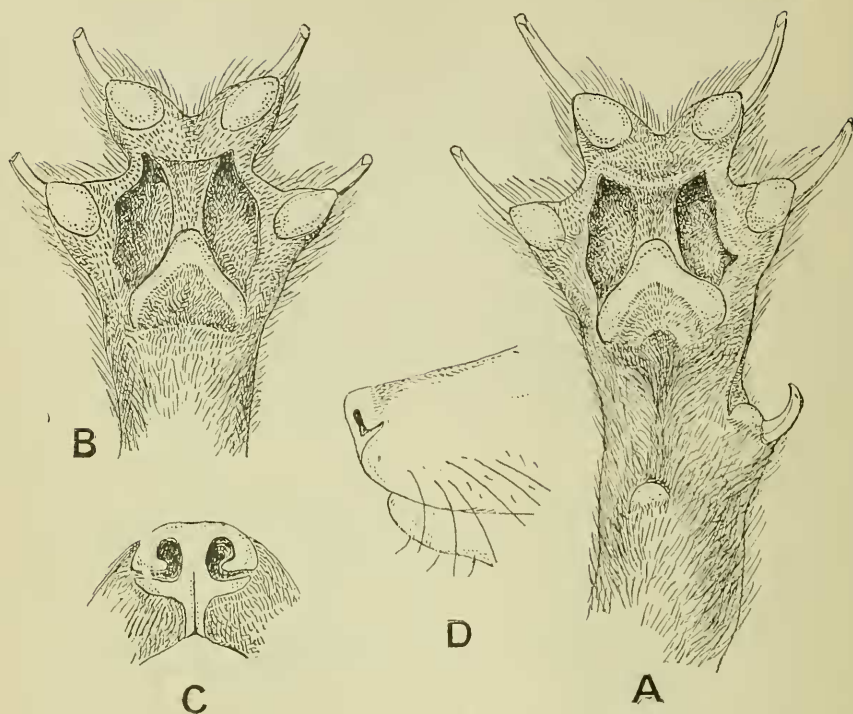
Alopex lagopus.

(Text-fig. 7.)

A single old female specimen of *A. lagopus spitzbergensis*.

The feet differ from those of all the species of Canidæ examined in the presence of a distinct thickish ridge of integument, passing forwards from the median lobe of the plantar pad to the area behind the point of junction of the third and fourth digits, and dividing the glandular depression between the digital and plantar pads into right and left portions. Moreover, the area of the integument on the proximal side of the digital pads is thickened and cushion-like, not gradually sloped away, so that the partially divided depression is bordered in front and laterally by elevated walls, making it appear deeper than in other species. The median longitudinal ridge of skin is not so high as the plantar pad and as the thickening behind the third and fourth

Text-figure 7.

*Alopex lagopus.*

A. Right fore foot.
B. Right hind foot.

C. Rhinarium from the front.
D. Rhinarium from the side.

digits, and, like the thickenings in question, it is clothed with longish hairs*.

The feet are shorter and more "dog-like" than in *Vulpes* and *Otocyon*, owing mainly to the third and fourth toes being shorter and a little more widely separable. The digital pads are small and the plantar pad is a little wider than in *Vulpes* and more overgrown posteriorly, so that it appears more deeply hollowed out. The carpal pad is nearer the plantar pad, and is small and irregularly semicircular in outline. Claws very long.

The *rhinarium* in profile view is nearly rectangularly pointed, and much shorter than in any other species examined. From the front view the summit is mesially nearly flat with widely-rounded angles; the inferior edge is not strongly angled, the

* In the specimen examined, an old female which had been over ten years in the Gardens, the hair on the integumental thickenings was worn off by walking on concrete. But the outline of the digital pads could be distinguished by their scaly pattern, the thickenings being pitted with hair-follicles.

nostrils are large and separated by a very narrow septum, and the groove from the upper lip extends upwards to a point just above the inferior border of the nostrils.

The *vibrissæ* are normal in position, and the mystacial and submental bristles are shorter than in *Vulpes* or *Canis mesomelas*.

Until Miller published his 'Catalogue of the Mammals of Western Europe,' the Arctic fox was not regarded as generically distinct from *Vulpes*, although Kaup and, later, Gray had applied generic names to it, because of the unsatisfactory nature of the characters by which it was distinguished. It cannot be claimed that the diagnostic features employed by Miller are of great value, as he himself seems prepared to admit. Most of them are cranial *, the only external feature mentioned being the shorter and more rounded ear. If such characters, however, be used for distinguishing "Alopecoid" genera, it will be necessary to give generic status to nearly every species of fox—using "species" in its old sense. Judged, however, by its feet, the Arctic fox is quite distinguishable generically from *Vulpes vulpes* and *bengalensis* and from *Otocyon*, and the same may be said of the rhinarium †.

In the extent of the area of the sole applied to the ground the feet of *Alopex lagopus* show superficial resemblance to those of *Speothos venaticus*, and a comparison between the two species suggests that the structural modification described as fusion of the pads in the latter is due to the nakedness of the integumental cushions behind the pads. But since in *Speothos* the naked areas regarded as pads are granular throughout, and show no trace of hair-follicles like the thickened integument behind the pads in *Alopex*, the view put forward in this paper, that the pads of *Speothos* are enlarged and fused, appears to be correct.

Vulpes vulpes Linn.

(Text-fig. 8, A.)

Feet long and narrow with comparatively small pads and long claws. Carpal pad small and set high above the plantar pad; and the digital pad of the first digit (pollex) above the middle of the area between the carpal and plantar pads.

Plantar pad moderately wide, but subcrenate in form, owing to the encroachment of the hair over its median portion posteriorly. Third and fourth digits especially long and tied together by a narrow web, so that the interval between them, when extended, is much less than the interval between the second

* One feature mentioned needs restating. It is said that the interorbital region of the skull is more elevated than in *Vulpes*, owing to greater inflation of the frontal sinuses. As a matter of fact, the frontal sinuses, as Huxley pointed out, are undeveloped, as in other "Alopecoid" skulls, the inflation in question being caused by the upward extension of the nasal passages.

† The caudal gland in the specimen examined was larger than in any species of Canidæ that I have looked at. It was a hairless patch of very thick glandular skin about 25 mm. long and one-third longer than wide. There was no underfur mixed with the hairs surrounding it; and, like the feet, it gave out a strong "foxy" smell.

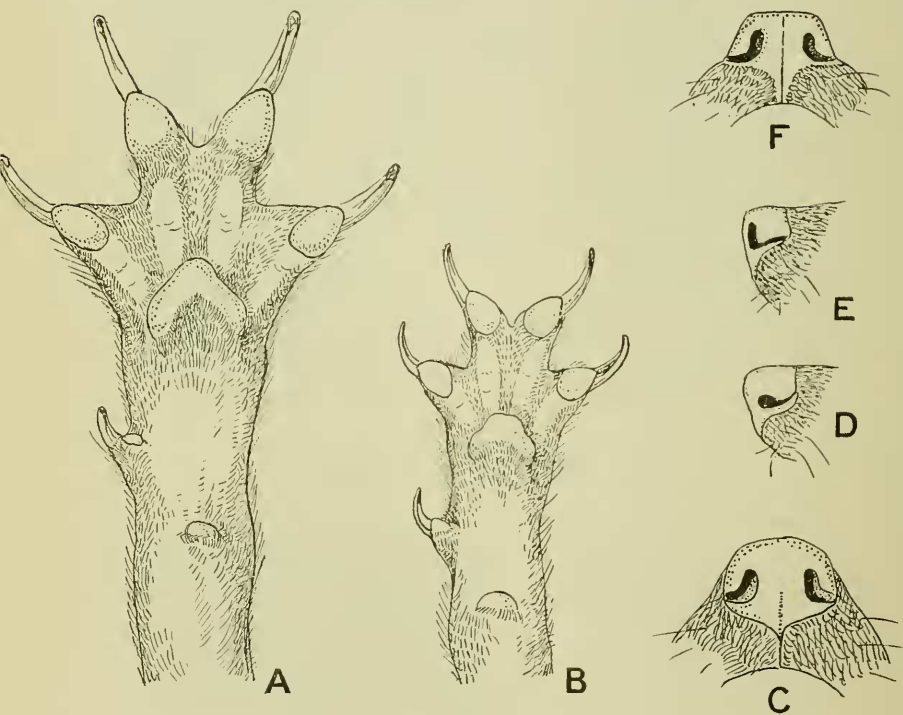
and third and the third and fourth digits. The length of the four digits makes the edge of the web connecting the median and lateral toes appear widely scooped out. The claws are long and the hair clothing the area between the digital and plantar pads is thick, but not long*.

Vulpes bengalensis Shaw.

(Text-fig. 8, B-D.)

The feet are similar in a general way to those of *V. vulpes*, but the third and fourth digits are, if anything, relatively longer

Text-figure 8.



Vulpes and *Otocyon*.

- | | |
|--|--|
| A. Left fore foot of <i>Vulpes vulpes</i> . | D. Rhinarium of same, from the side. |
| B. Left fore foot of <i>Vulpes bengalensis</i> . | E. Rhinarium of <i>Otocyon megalotis</i> ,
from the side. |
| C. Rhinarium of same, from the front. | F. The same, from the front. |

* The hairiness of the soles of the feet may vary seasonally in this species, as it does in some of the northern Canidae. Very likely, too, variation in this respect will be found between geographical races of *V. vulpes*.

and the second and fifth shorter. The carpal pad is relatively larger, the posterior region of the plantar pad is less overgrown with hair, and the hairs arising just behind the digital pads are exceedingly long and project forwards beneath the pads as far as the tip of the long slender claws.

The *rhinarium* is slightly acutely rounded in profile view anteriorly; from the front its upper edge is tolerably evenly curved and its inferior border only slightly angled mesially, the area below the nostril being moderately deep in front and narrow below the slit posteriorly.

The *facial vibrissæ* are long and normal in position.

Otocyon megalotis Desm.

(Text-fig. 8, E, F.)

In all essential respects the feet of this fox, accorded generic rank mainly by reason of its abnormal dentition, agree with those of *Vulpes vulpes* and *bengalensis*, although the third and fourth digits are a little shorter. The median lobe of the plantar pad is a little more prominent, especially as compared with that of *V. bengalensis*, and its posterior border is emarginate by the growth of hairs as in that species. The carpal pad is very small.

The *rhinarium* is slightly elevated above and rectangularly rounded anteriorly in profile view; seen from the front its upper edge is straight with obtusely rounded angles and its lower edge is angular, the portion below the nostrils being shallow and very narrow laterally and posteriorly below the slit.

The *facial vibrissæ* are normal in position and moderately long.

CONCLUSION.

Although only a few species of Canidæ, compared with the numbers known, have been described in the foregoing pages, they fortunately represent the main groups of generic or subgeneric rank into which the family has been divided. It is probable therefore, I think, that the extremes of variation in the structure of the feet, in the shape of the rhinarium, and the disposition of the vibrissæ have been observed.

It does not appear to me to be likely that the broad distinction between *Speothos* and the rest will be lessened by the examination of other species—and probably *Lycæon* and *Cuon*, and possibly *Alopex*, will also remain isolated; but it would be rash to assume in the present state of our knowledge that the differences in foot-structure between the species recorded under *Pseudalopex*, *Cerdocyon*, *Canis*, and *Vulpes* will hold good in all cases when the species related to them come to hand for examination. That, however, remains to be seen.

In the meantime, it may be useful to tabulate the results so far achieved to show briefly how the species may be grouped, and to draw attention to the more salient characters presented by the feet. In the following table, however, I have only made

use of the fore feet, partly in the interests of brevity, partly because they supply the best characters, and partly because the features presented by the vibrissæ and rhinarium call for verification on fresh material, which is unavailable at the present time :—

- a. Pad of pollex set low down close to the posterior lateral angle of the plantar pad; pads of third and fourth digits basally united; edge of web between median and lateral digits naked; area between digital and plantar pads and between carpal and plantar pads scantily covered with short hair *Speothos venaticus*.
- a'. Pad of pollex, when present, high above plantar pad; pads of third and fourth digits separated; edge of webs joining the median with the lateral digits hairy; area between digital pads and plantar pad and between the latter and the carpal pad mostly thickly hairy.
- b. Edge of web joining third and fourth digits naked, forming a definite hairless band; a long fringe rising behind this and extending round the periphery of the foot behind the digital pads.
- c. Pollex suppressed, feet long, carpal pad high above plantar pad *Lycæon pictus*.
- e'. Pollex retained; feet shorter, carpal pad moderately high above plantar pad..... *Canis primævus*.
- b'. Edge of web between third and fourth digits hairy.
- d. Glandular depression between pads undivided; integument proximal to the pads not specially thickened.
- e. Third and fourth digits exceedingly widely separable, the edge of their web when stretched forming a straight line about twice the length of the pads of either digit; plantar pad long and narrow *Pseudalopex gracilis*.
- e'. Third and fourth digits much less widely separable, the edge of the web between them emarginate when stretched and less than the length of the pad of either digit.
- f. Plantar pad large, its width exceeding the length between its median lobe and the margin of the web between the shorter third and fourth digits; claws short.
- g. Carpal pad very small, third and fourth digits more widely separated, the web joining them, when extended, as wide as that between them and the lateral digits *Cerdocyon microtis*.
- g'. Carpal pad large, third and fourth digits more closely united; the connecting web narrower than that between them and the lateral digits... *Canis anthus, mesomelas**.
- f'. Plantar pad small, its width considerably less than the distance between its median lobe and the edge of the narrow web between the long third and fourth digits; claws long *Vulpes vulpes* and *bengalensis*; *Otocyon megalotis*.
- d'. Glandular depression between digital and plantar pads divided by a ridge of thick skin stretching forwards from the median lobe of the plantar pad; integument surrounding proximal portion of digital pads much swollen and cushion-like; feet otherwise almost as under e' *Alopex lagopus*.

The above-given analysis of the characters of the feet of the Canidæ emphasises the distinctness of *Speothos* from the rest of the genera, and does not afford support to the affiliation of *Speothos*

* The feet of domestic breeds of dogs come under this heading. The feet of some breeds indeed conform very closely to the type seen in *Canis anthus* (see P. Z. S. 1914, pp. 478-484).

with *Cuon* and *Lycaon* in the *Cuon*-group opposed to the *Canis*-group containing *Canis*, *Vulpes*, and *Otocyon* *.

On the contrary, the distinctness of *Speothos* may, I think, be justifiably expressed by setting the genus aside in a special subfamily, the *Speothoinæ*, the remaining genera being called *Caninæ*.

There is, as yet, no agreement respecting the number of genera into which the Canidæ are divisible, but all recent zoologists are in accord in admitting *Lycaon*, *Cuon*, *Canis*, *Vulpes*, *Otocyon* and probably *Nyctereutes* and *Urocyon*. Both *Vulpes* and *Canis* have been further subdivided into many genera or subgenera. Thomas †, for instance, has recently shown that, apart from *Speothos*, the following South American dogs have been generically named as follows:—*Chrysocyon* for *jubatus*; *Dasicyon* for *antarcticus*; *Cerdocyon* for *thous* (= *carnivorius*) and *brasiliensis* (= *azare*); *Pseudalopex* for *magellanicus*, *azaricus*, etc., and *Lycalopex* for *vetulus*. At present, however, these genera are, I believe, merely nominal, in the sense of being undefined. There will be time enough to discuss their validity when the distinctive features have been ascertained and stated; and the same may be said for such subdivisions of *Vulpes* as *Fennecus* and *Zerda*. Possibly extended study of the feet and other external features may help the settlement of this difficult question.

Family URSIDÆ ‡.

The subjoined account of the feet and the noses of the Ursidæ is based upon the examination of examples of the following species that have died in the Gardens, namely, the Polar Bear (*Thalartos maritimus*), the American Black Bear (*Ursus americanus*), the Himalayan Bear (*Tremarctos thibetanus*), and the Sloth Bear (*Melursus ursinus*); and secondly, upon observations on living examples in the Society's menagerie and upon dried skins in the British Museum. The four species in question exhibit the extreme range of variation in the structure of the feet, the Polar Bear and the Sloth Bear being at opposite poles in the matter of modification; and all the other existing species of bears agreeing, apart from minor details, either with *U. americanus* or with *T. thibetanus*.

The general shape of the feet of bears is well known. Measured from the carpus or the tarsus to the tips of the phalanges, they are remarkably short and broad. The five digital pads form a slightly curved line, the second, third, and fourth being nearly on a level and a little in advance of the first and fifth. A short distance behind these pads, and separated from them by a comparatively thin-skinned depression, comes the wide

* By Matthew and Osborn ('The Age of Mammals,' 1910). I do not, however, know the nature of the evidence on which this classification was based.

† Ann. Mag. Nat. Hist. (8) vol. xiii. p. 352 (1914).

‡ For the generic terms adopted for this family see *infra*, pp. 939-940.

and flattish main or plantar pad*. Behind the plantar pad of the fore foot there is always one additional carpal pad on the external or ulnar side of the carpus; and on the hind foot there is always a larger or smaller naked area, which may involve the whole of the posterior portion of the sole as far back as the heel. It is mainly, however, in the degree of hairiness of this area behind the plantar pads of both fore and hind feet that the greatest variation is exhibited.

Feet of the Polar Bear (Thalarcos maritimus).

(Text-fig. 9, A, B.)

In two newly-born cubs of Polar Bears from Spitzbergen, the digital pads are not webbed, but are separated to the base as in all bears except *Melursus*. The depressed area between them and the very short and wide plantar pad is scantily covered with very short hairs, and the area behind the plantar pad is similarly covered, except for the small external carpal pad on the fore foot and a corresponding, elongated, somewhat piriform, anteriorly pointed, small, flat pad on the sole of the hind foot, which are quite naked.

In our adult living examples the soles of the feet, apart from the digital and plantar pads, the carpal pad, and the corresponding elliptical area on the hind foot, are thickly covered mostly with long hair, except the sole of the hind foot, where the hair is worn short; and in a male specimen a narrow strip of naked skin extends forwards from the naked elliptical area to the plantar pad of the hind foot. The feet, in fact, agree with the description of the feet of the Polar Bear, recently published by G. S. Miller †, who says:—"Fore feet with palmar tubercles and balls of toes essentially as in *U. arctos*, but smaller; pad on hind foot without backward continuation along inner [outer] portion of sole." Since Miller did not detect the little naked pad behind the plantar pad on the hind foot, it is possible that this pad is sometimes, perhaps seasonally, covered with hair. But its presence in this newly-born cub is full of significance.

Feet of the Black Bear (Ursus americanus).

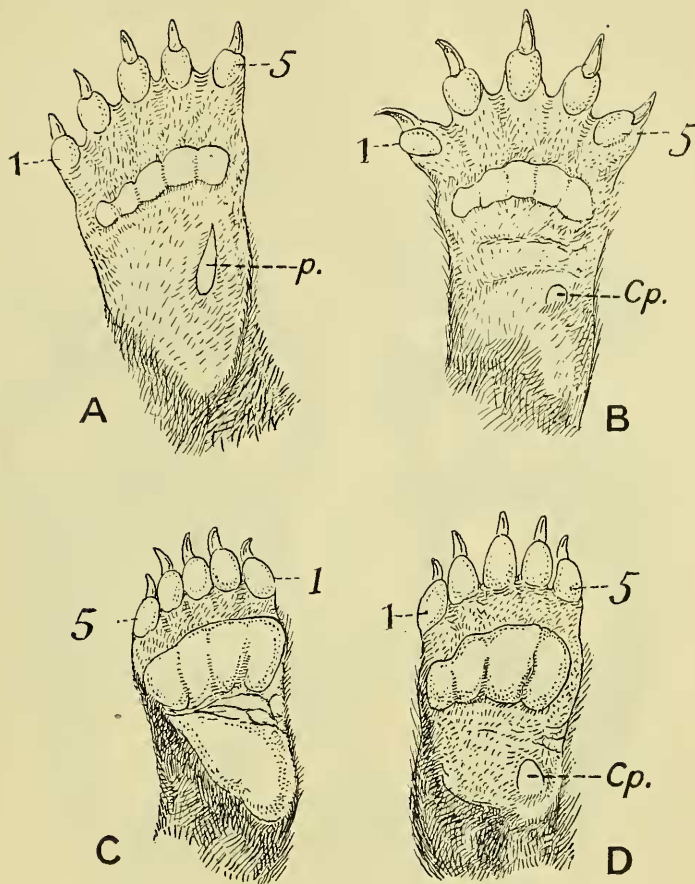
(Text-figs. 10 and 13, D, F.)

The fore feet of an adult male Black Bear from Newfoundland agree in essential points with those of the Polar Bear, that is to say, the digital pads are separated, the depression behind them is covered thickly with long hairs, and the area behind the plantar pad is similarly clothed with hairs, from which the carpal

* It is the custom sometimes to call the main pad of the fore foot the "palmar" and that of the hind foot the "plantar" pad. But in this paper I have used the term plantar for the main pads of both fore and hind feet.

† Cat. Mamm. Western Europe, p. 298, 1912. In his description of the hind foot of this species, as of *U. arctos*, Miller wrote "inner" for "outer."

Text-figure 9.



Newly-born cubs of Polar Bear (*Thalarectos maritimus*) and of European Brown Bear (*Ursus arctos*).

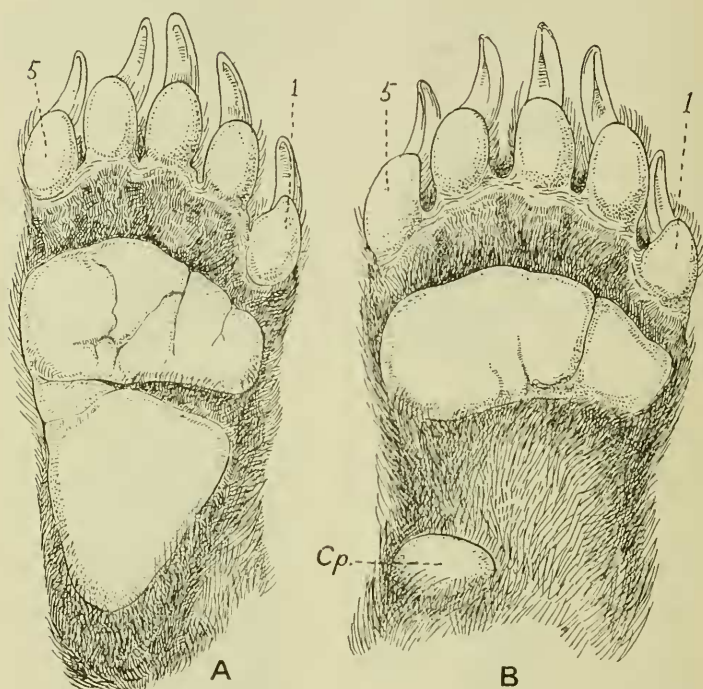
- A. Left hind foot of Polar Bear (*Thalarectos maritimus*), the digits spread. C. Right hind foot of Brown Bear (*Ursus arctos*).
 B. Left fore foot of same. D. Left fore foot of same.

1 and 5, first and fifth digits; *Cp.*, carpal pad; *p.*, pad on sole of hind foot of *T. maritimus*.

pad rises like an island. But this pad, the digital pads, and especially the plantar pad are relatively large. The hind foot, however, is very different, in being mostly naked almost back to the heel. On the inner or hallucal side, however, the hair grows inwards from the edge of the foot for a short distance behind

the plantar pad, filling up the depression which at this point separates this pad from the posterior naked part of the sole.

Text-figure 10.



Ursus americanus.
 A. Right hind foot. B. Right fore foot.
 1 and 5, first and fifth digits; *Cp.*, carpal pad.

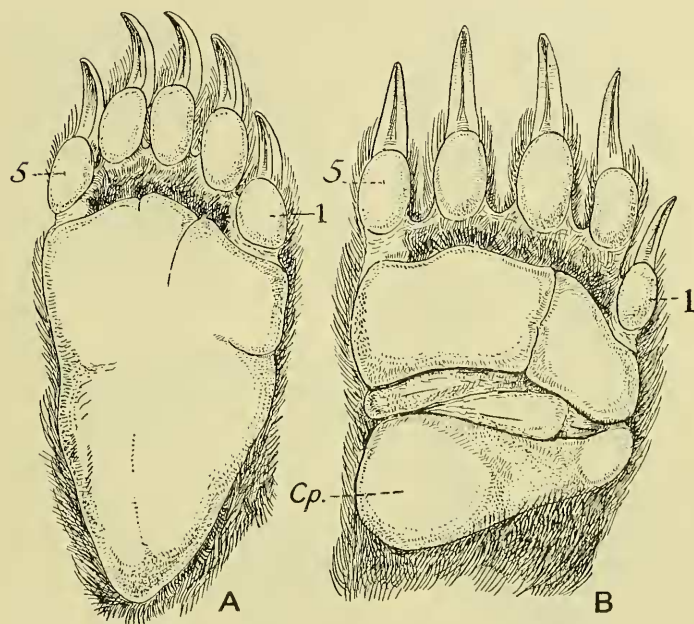
Feet of the Himalayan Bear (Tremarctos thibetanus).
 (Text-figs. 11 and 13, C.)

The fore feet differ markedly in one or two points from those of the Black Bear. The area between the digital pads and the plantar pad is hairy only behind the pads of the second, third, and fourth digits; behind the first and fifth of these pads it is naked and the digital pad of the first is smaller and set still farther back, its distal end scarcely reaching the proximal end of that of the second. The plantar pad is large. Behind it there is a naked depression of thinner skin and the carpal region is also wholly naked, the ulnar carpal pad forming a large protuberance and the radial a smaller one. This smooth carpal area

is sharply circumscribed behind by the dense clothing of hair covering the lower side of the leg.

The hind foot broadly resembles that of *U. americanus*, except that the depression behind the digital pads is clothed with hairs in the same way as the fore feet and the hairs from the inner edge do not encroach upon the sole in the depression marking off the plantar pad postero-internally. The tips of the pads of the first and fifth digits slightly overlap the proximal ends of those of the second and fourth respectively.

Text-figure 11.



Tremarctos thibetanus.

A. Right hind foot.

B. Right fore foot.

1 and 5, first and fifth digits; Cp., carpal pad.

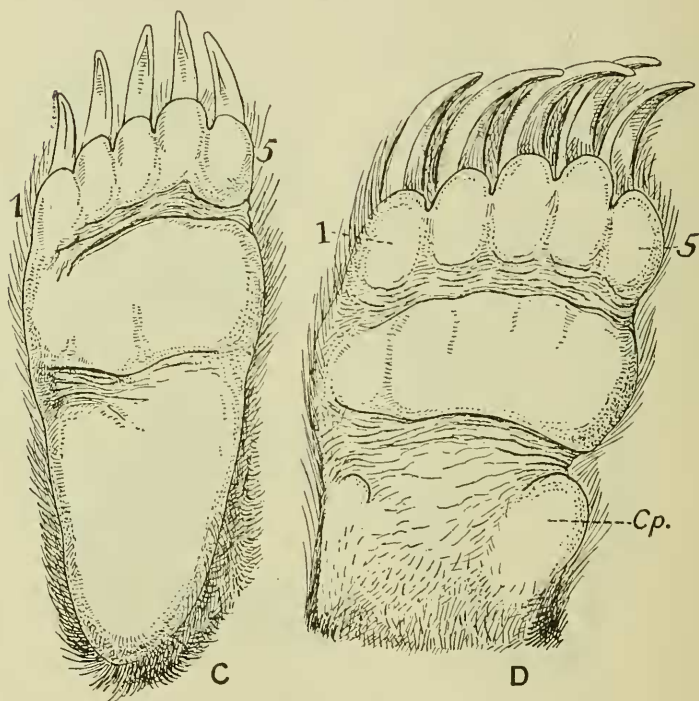
Feet of the Sloth Bear (Melursus ursinus).

(Text-figs. 12 & 13, A, E.)

The feet differ from those of all other species of Ursidæ, in that the digital pads are fused almost to their distal ends, so that no hair projects between them from the sides of the digits, and the first and fifth digits are set far forwards as compared, at all events, with *T. thibetanus*. Moreover, the depression behind the the digital pads is quite naked, as Gray pointed out. In the fore feet the carpal area is naked, as in

T. tibetanus, but this naked area is not sharply defined behind by a coating of thick hair, but passes insensibly into the skin of the posterior surface of the leg, which inferiorly is scantily clothed with short hairs. The sole of the hind foot is entirely naked, the posterior limit of the plantar pad being marked by a transverse groove, which expands into a shallow depression on the hallucal or inner side.

Text-figure 12.

*Melursus ursinus.*

C. Left hind foot (too narrow for its length).

D. Left fore foot.

1 and 5, first and fifth digits; Cp., carpal pad.

Feet of other Species of Bears.

The feet of the Polar Bear and of the Sloth Bear are unique in the family, but those of other species, of which I have only seen dried skins or living specimens, agree in the main with those either of *T. tibetanus* or of *U. americanus*, *U. arctos* and *horribilis* falling into the same category as *U. americanus* and *Helarctos malayanus*, and *T. ornatus* into that of *T. tibetanus*.

G. S. Miller* describes the feet of the Brown Bear of Western Europe as follows:—"Balls of the digits [of fore feet] large, pad-like . . . first digit with anterior edge of ball extending about to middle of that of second, the interval greater than in the case of the other digit . . . main pad wider than long, covering more than half the surface of the palm, its outer border about twice as long as its inner, its posterior border slightly concave, its inner portion at base of thumb [1st digit] marked off from the rest by a slight furrow; region between main pad and balls of digits densely furred; wrist-pad about as large as ball of digits, near outer ulnar margin of palm, its long diameter transverse; region between wrist-pad and main pad densely furred . . . Hind foot longer than fore foot, pad like that of fore foot, but with a broad backward extension passing along inner [outer] side† nearly or quite to heel; region between pad and balls of toes and at outer [inner] side of backward extension densely furred."

In a newly-born cub of *U. arctos* (text-fig. 9, C, D, p. 931), the area between the digital and plantar pads of both fore and hind feet is scantily covered with very short hairs, the posterior or heel pad of the hind foot is naked, and there is a well-marked depression of wrinkled skin on the inner side of the foot between this pad and the plantar pad. In the fore foot the area behind the plantar pad is scantily clothed with short hairs, and the conical carpal pad is situated near the postero-external portion of this area.

So far as I have been able to examine them, the living bears of this species in the Gardens, namely examples from the White Sea, Caucasus, Himalayas, Behring Sea, and Alaska, have the feet as above described by Miller, except that the entire sole of the hind foot is generally naked, there being usually no extension of the hair behind the plantar pad on the inner side. In some Brown Bears, too, there is a narrow strip of scantily-haired skin extending from the carpal pad to the plantar pad of the fore foot, and sometimes a small naked area marks the position of a radial carpal pad. These points may be worth further investigation from the systematic point of view.

In one of two Grizzly Bears (*U. horribilis*) from Montana, the feet seem to resemble those of our Brown Bears; and Mr. Seton's figure of the paws of the Grizzly show the same conformity to the Brown Bear type.

The chief difference between the feet of *U. americanus*, on the one hand, and *U. arctos* and *horribilis*, on the other, is that in the former the first digit and the carpal pad seem to be set farther back.

Tremarctos thibetanus ranges from Baluchistan to Eastern Asia, and is represented in Japan by *T. japonicus*, which is probably

* Cat. Mamm. Western Europe, p. 287, 1912.

† The sole is continuous along the *outer*, not along the *inner* side of the foot. The hairy ingrowth interrupting the continuity of the sole occurs on the *inner* or hallucal side.

only a subspecies of it. At all events, the feet are the same in the two forms.

Moreover, the feet of the Malayan Bear (*Uelarcos malayanus*) agree in all essential respects with those of *T. thibetanus*, except that the hairs in the depression behind the second, third, and fourth digital pads are much fewer in number, the integument being scantily furred, and thus approximating the naked condition of this area seen in *Melursus*. The Andean Bear (*T. ornatus*) also resembles *T. thibetanus* in the structure of its feet, except that the depression behind the digital pads is continuously and thickly hairy, even behind the pads of the first and fifth digits.

Structural Adaptation of the Feet to Habits.

The bionomical reason for the differences in the structure of the feet of existing Ursidæ is obscure. The first thing to note is the rough correspondence between the hairiness and nakedness of the sole and the geographical latitudes inhabited by the species. The hairiest feet of all are found in the Arctic species (*Thalarcos maritimus*), and this feature is always assumed, probably correctly, to be a modification to obviate the likelihood of slipping on ice. But it must also be remembered that the haunts of this bear are treeless, and that this species is unable to climb. South of the range of the Polar Bear come the various races of *Ursus arctos*, of *U. horribilis*, and of *U. americanus*, which have larger pads on the fore and hind feet than in *Thalarcos maritimus* and the greater part, at all events, of the sole of the hind feet naked. Even the northern form of these species, by reason of their hibernation, are never abroad for any length of time when the cold is severe enough to cover the ground for weeks at a time under a continuous sheet of frozen snow. The countries they inhabit are forested, and both the Black and the Brown Bears are known to climb trees. The Grizzly does not climb—at all events, as a rule,—but he probably could do so, if necessary, though, on account of his greater bulk, not with such ease as the Black Bear and smaller representatives of the Brown Bear. Nevertheless, neither the Black Bear nor the Brown Bear seems to be so apt at climbing as the three naked-footed bears of the Old World, namely, the Himalayan, the Malayan, and the Sloth*; and living examples of these species have an obviously clumsier, more shuffling gait than the northern species, and this awkwardness of movement is due very largely, if not wholly, to the natural inturning of the fore feet.

* I know nothing of the Andean Bear (*U. ornatus*) in this connection. Of the Himalayan Brown Bear (*U. arctos isabellinus*), Blanford says:—"They can climb trees, but, in the Himalayas, at all events, rarely do so"; of the Himalayan Bear, "it is more in the habit of climbing trees for fruit [than the Brown Bear], and is not infrequently found in fruit trees," and of the Malayan species "this bear is a purely forest animal and an admirable climber," while his account of the Sloth Bear contains many references to its scansorial habits.

This characteristic of the limbs is more marked in the Malayan and the Sloth Bear than in the Himalayan, which in this, as in other respects, comes nearer the group of bears typified by *U. arctos*. I think it probable that the nakedness of the carpal area of the underside of the fore foot in those three species as well as the inturning of the paws are adaptations to climbing, because naked roughish integument will give a better hold on bark than integument covered with hairs, and during the ascent or backward descent of a vertical tree-trunk—bears always climb down rear end foremost—the upward turn of the fore paws gives the claws a securer grip on the bark, because their points are set at right angles to the axis of the trunk, without interfering with the clasping action of the limb.

Noses of Bears.

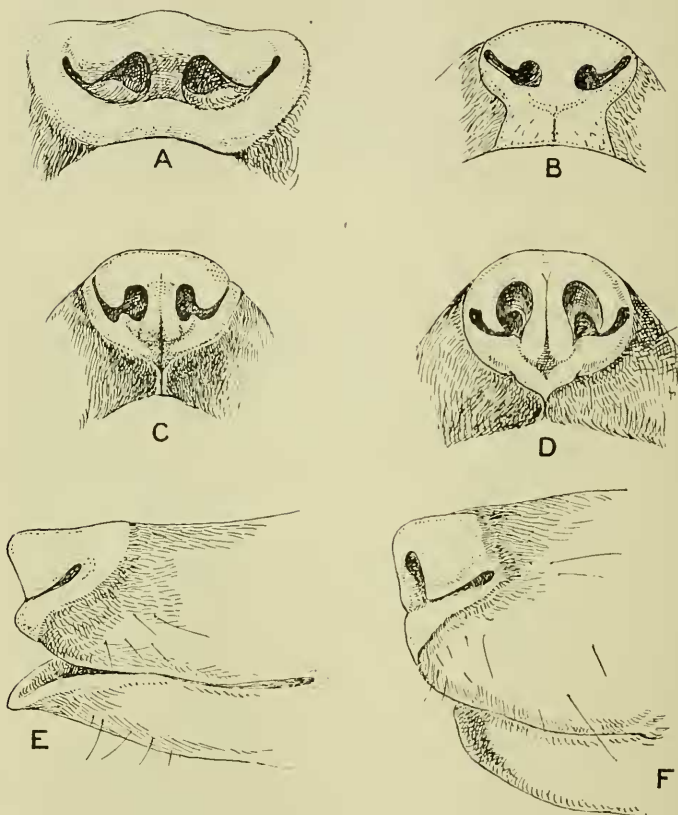
The rhinarium of Bears is always large and naked, and is circumscribed above and at the sides by the short hairs of the muzzle and upper lips. Usually the hair on the summit of the muzzle forms nearly a straight line, passing from the posterior notch of one nostril to that of the other; and beneath the rhinarium the hairs of the upper lip extend almost or quite to the middle line, leaving at most a narrow strip of naked integument below the rhinarium. I have not been able to examine sufficiently closely a large enough number of specimens to show the variation in width to which this strip of integument is liable in *Ursus arctos*, *horribilis*, *americanus*, *Tremarctos thibetanus*, *ornatus*, but in all these species, as in *Thalarcos maritimus*, it is at most a few millimetres wide, narrower, that is to say, than the median area of the rhinarium between the inner edges of the nostrils.

But in the Sloth Bear (*Melursus*) the rhinarium is very large. Dorsally it extends forwards so as to overhang the nostrils and backwards some distance behind the posterior end of the slit of the nostrils. It is also much wider beneath the slit laterally and there is a very wide median area of moist skin annexed to the rhinarium on the upper lip. The only bear possessing a rhinarium approaching that of *Melursus* in relative size is *Helarctos malayanus*, which, in this respect, is intermediate between *Tremarctos thibetanus* and *Melursus ursinus*. In both these species the greater size of the rhinarium and of the moist naked area below it, is associated with the mobility of the snout and upper lip, which is a marked feature in *Helarctos malayanus* and reaches an extreme in *Melursus ursinus*.

The *facial vibrissæ* of Bears are reduced in number and length, as compared with those of most other Carnivores. A few buccal and superciliary bristles are retained, but the genals and interramals appear to be suppressed as a rule. The genals I did not find in any of the dead specimens examined, but in the example

of *T. thibetanus* the interramal tuft was represented by a single longish hair.

Text-figure 13.



Rhinaria of Bears.

- | | |
|----|--|
| A. | Anterior view of rhinarium of <i>Melursus ursinus</i> . |
| B. | Ditto <i>Helarctos malayanus</i> (from a dried skin). |
| C. | Ditto <i>Tremarctos thibetanus</i> . |
| D. | Ditto <i>Ursus americanus</i> . |
| E. | Side view of lips and rhinarium of <i>Melursus ursinus</i> . |
| F. | Ditto <i>Ursus americanus</i> . |

Systematic Value of the Feet.

From time to time the Ursidæ have been split up into a considerable number of genera and subgenera, based partly upon external, but mainly upon dental and cranial characters, the only well-marked species which has never apparently received a special

title, even from Gray, being *U. thibetanus*. For instance, we have *Thalarcos* (usually altered to *Thalassarcos*) for *maritimus*; *Ursus* for *arctos* and its allies, *Danis* for *horribilis*, *Euarctos* for *americanus*, *Tremarctos* for *ornatus*, *Helarctos* for *malayanus*, and *Melursus* for *ursinus*. *Melursus* seems to be admitted on all hands as valid; but probably no two existing zoologists could be found to agree about the others, though a majority would most likely favour the severance of *Thalarcos* from *Ursus*. Flower and Lydekker ('Mammalia Living and Extinct,' pp. 558-560, 1891), for example, gave full generic value to *Melursus* and to *Ursus*, and divided the latter into the *Thalarcetine* section for *maritimus*; the *Ursine* for *arctos*, *horribilis*, *americanus*, *thibetanus*, *ornatus* and their allies, and the *Helarctine* section for *malayanus*. Max Weber (Die Säug. p. 535, 1904) admitted *Ursus*, with *Thalarcos* as a subgenus, *Helarctos* and *Melursus*, but only diagnosed the latter; and Beddard ('Mammalia,' pp. 442-443) allowed *Ursus* and *Melursus*, dismissing *Thalarcos* as a "quite unnecessary" genus.

Trouessart (Cat. Mamm. Suppl. pp. 178-182, 1904) followed Flower and Lydekker in the main, but gave subgeneric value to the sections of *Ursus*, adding *Euarctos* to them, and accorded full generic status to *Tremarctos* for the S. American Bears.

Finally, Matthew and Osborn ('The Age of Mammals,' p. 530, 1910) adopted the four genera, *Ursus* for the Grizzly, Brown, and American Black Bears, and, I presume, for the Himalayan and Malayan as well, *Thalarcos* for the Polar Bear, *Tremarctos* for the Andean or Spectacled Bear, and *Melursus* for the Sloth Bear.

The divergence of opinion with respect to the status of such species as *maritimus*, *americanus*, *ornatus*, and *malayanus*, indicated by these classifications, suggests that the characters used for their elevation to the rank of genera or subgenera cannot be very well marked*. But in view of the conclusions arising from the facts established in this paper, the one interesting point about which these authors seem to be in accord, differ as they may about the four species just quoted, is that *thibetanus* is inseparable from *Ursus*, even in the most restricted sense assigned to that term.

Beyond stating that the soles of the feet are more hairy in the Polar Bear, the authors above quoted made no systematic use of the extremities, although Gray had previously pointed out some distinguishing features presented by them†. He detected,

* The classifications of Trouessart and of Osborn & Matthews are, however, mere lists of names, no reasons for the arrangement adopted being given. It would be interesting to know why these authors, alone of those quoted, give full generic value to *ornatus*.

† Considering the wide field covered by his work, J. E. Gray was head and shoulders in front of many of his predecessors and successors as a systematist in the strict sense of the word. One is too apt to allow his mistakes, arising from his curious limitations, to obscure one's regard for the perspicacity he undoubtedly possessed in the detection of structural differences.

for instance, that the area behind the digital pads in the Sloth Bear is naked, whereas it is hairy in others. But he does not appear to have noticed the marked differences presented by the carpal area in the matter of hairiness and nakedness in various species, and his statement that in *Thalassarctos* the "soles of the feet are hairy with a few callous pads, whereas in *Ursus*, *Helarctos*, and *Melursus* they are bald and callous," gives very little idea of the true state of affairs (see Cat. Carn. etc. Mammalia, pp. 217-237, 1869).

Judged by the characters discussed in this paper, the following genera seem to me worthy of admission—*Melursus*, *Helarctos*, *Tremarctos*, *Ursus*, and *Thalarctos*. They may be defined as follows:—

- | | |
|--|---------------------|
| a. Digital pads fused almost up to their distal ends, depression between them and the plantar pad of both fore and hind feet naked; carpal area of fore paw naked with large rounded external and smaller internal pads; integument of fore leg behind carpal area scantily covered with short hairs; snout highly mobile, rhinarium very large, extending to edge of lip as a broad moist area and overhanging the nostrils above | <i>Melursus</i> . |
| b. Digital pads separated throughout their length, depression between them and the plantar pads more or less hairy; integument behind carpal area thickly covered with hair; snout less mobile, rhinarium smaller and not overhanging the nostrils. | |
| c. Carpal area as in <i>Melursus</i> , naked and furnished with a larger rounded external and a smaller internal pad. | |
| d. Hair on upper lip not extending beneath the nostrils in front, but leaving a comparatively wide moist median area continuous with the rhinarium above | <i>Helarctos</i> *. |
| d'. Hair on upper lip extending nearly to middle line and leaving only a narrow naked strip of skin continuous with the rhinarium | <i>Tremarctos</i> . |
| e. Carpal area behind plantar pad thickly hairy, carpal pads represented by a single rounded eminence on the outer side, as in the Canidae and Felidae, and sometimes by a smaller one as well on the inner side; rhinarium approximately as in <i>Tremarctos</i> . | |
| e. Pads large as in the preceding genera: sole of hind foot behind the plantar pad naked, except sometimes for an ingrowth of hair internally behind the plantar pad | <i>Ursus</i> . |
| e'. Pads smaller: sole of hind foot behind plantar pad overgrown with hair except for a small naked flat pad near the external border | <i>Thalarctos</i> . |

Melursus, *Helarctos*, and *Thalarctos* are monotypical. *Tremarctos* contains two well-defined species, namely *thibetanus* and *ornatus* (type), which I cannot distinguish externally by any characters of generic value in my opinion. Nevertheless, the difference in the smoothness of the integument behind the first and fifth digital pads in *thibetanus* and its hairiness in *ornatus* is very curious. *Ursus* contains a doubtful number of species and subspecies, but I am not acquainted with any external features

* This genus, or subgenus, is usually defined by the shortness and breadth of the skull, smallness of the ears, length of the tongue, etc.

justifying the admission of *Danis* (type *horribilis*) and *Euarctos* (type *americanus*), unless the more backward position of the first digit in the fore paw of *americanus* and the higher position of the carpal pad be given generic value—in my opinion, an exaggerated view of their importance*.

As regards the genealogical position of the genera judged from their feet, analogy justifies the opinion that the naked-footed forms with free digital pads, like *Helarctos* and *Tremarctos*, are the more primitive†. From a stock probably resembling these in the particulars named, *Melursus* is specialised on one side by the fusion of the digital pads and *Ursus* on another side by the growth of hair over the carpal region. *Thalarctos* appears to me to be nothing but a specialised type of *Ursus*, adapted for swimming and movement on ice, its longer and more powerful canine teeth being developed for the seizing and slaying of seals.

* Merriam admits *Euarctos* as a subgenus of *Ursus* on account of certain cranial and dental differences. *Danis*, however, appears to be undefinable (Proc. Biol. Soc. Wash. x. pp. 65, 83, 1896).

† In the bears themselves this view finds support in the scantiness and shortness of the hairs clothing the areas behind the digital and carpal pads in the newly-born cubs of *Thalarctos maritimus* and *Ursus arctos*.
